THE NEST OF *POLYRHACHIS AUSTRALIS* MAYR (HYMENOPTERA: FORMICIDAE)

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Abstract

Many species of the large ant genus *Polyrhachis* F.R. Smith make nests using silk from their own larvae or from spiders. This paper reports on 400 nests of *Polyrhachis australis* Mayr dissected at Townsville, Queensland, between 2009 and 2015. Details are given of host plants, nest structure, materials used (carton and silk), placement of brood within nests, resistance to disturbances such as rain and nest longevity. Carton nests are typically lined with flat-sheet silk. Complex internal structure gave more internal surface area, so absolute nest size is not a reliable indicator of ant numbers. Occasional use of fluffy spider-silk in outer walls led to more flaccid nest structure. Use of a sticky, ductile form of silk, probably derived from moths, was also identified. Dedicated brood chambers were not noted, but brood clumping was usual, possibly representing offspring of different queens. Brood was attached to the nest substrate by diffuse silk strands. Individual nests could persist for 15 months and grew little after an initial period of expansion.

Introduction

The exceptionally wide variety of nesting habits in the species-rich ant genus *Polyrhachis* Fr. Smith was first reported by Jacobson and Wasmann (1905) and has since been the subject of many investigations and reports (*e.g.* Ofer 1970, Hölldobler and Wilson 1983, Dorow and Maschwitz 1990, Robson and Kohout 2005, 2007, Robson *et al.* 2015, Tranter and Hughes 2015), while the use of silk in nest construction has been documented in at least 264 *Polyrhachis* species (Liefke *et al.* 1998). There are two confirmed sources of the silk: from spiders and from larvae of the ants themselves (Robson and Kohout 2007). Spider silk in nests was reported by Collart (1932) for *P. laboriosa* F. Smith, Dwyer and Ebert (1994) for *P. australis* (as *P. doddi* Donisthorpe) and *P. pilosa* Donisthorpe, and Robson (2004) for *P. turneri* Forel. Dwyer and Ebert (1994) reasoned that using spider silk as a first option in the construction of nests may be the norm for arboreal *Polyrhachis* weaver ants, since queens establishing nests independently (haplometrotically) have no larvae with them, while those establishing nests dependently (*i.e.* with worker assistance) often rely on the workers setting up the nests before any queens arrive; those workers may not import larvae until shelter is sufficient. Nests can be initiated by fewer than 20 workers in these cases and may be located preferentially where spiders are sheltering (Dwyer and Ebert 1994).

Polyrhachis australis, whose original habitat is rainforest and woodland margins (CSIRO 2010), has adapted to the semi-natural suburban environment of humans, nesting in gardens that are dense, moist and shady.

Methods

Between September 2009 and December 2012, 220 *P. australis* nests were collected in Townsville, northern Queensland (Australian dry tropics, 19°18′S, 146°45′E) and their contents recorded. That study (Downes 2015)

documented seasonality in numbers and life history stages of the weaver ants. From 2013 to 2015, another 180 nests were examined. Descriptions of the structure and dynamics of all 400 nests are presented here.

External nest dimensions (missing data 45, n = 355) were taken to estimate nest size (volume), using the protocol of Downes (2015). Details of the internal structure were noted during nest dissections. Carton and silk, the major external and internal constituents other than the supporting architecture (leaves of the host plants, for the most part), drew particular attention, especially in the later years of the study. Three-dimensional flocculent masses of fibres, distinct from the flat sheets of silk lining the interior, were assumed to be spider silk, following Dwyer and Ebert (1994), Robson (2004) and Robson and Kohout (2005, 2007, 2008).

Host plants were recorded from May 2013 onwards, but these records must remain anecdotal: corresponding data on host plant frequency in the habitat would be needed to quantify preferences.

Between August 2013 and March 2015, 63 nests were tagged *in situ* and their growth, decline and fates monitored regularly (weekly or more often).

Results
Host plants
Nests were situated not only on or between leaves (Figs 1-2), but also under bark or within the hollows of stems. Banana plants (*Musa* sp., Musaceae) afforded retreats of the latter kind; likewise the tough, tubular woody fronds of the Cocos or Queen palm, *Syagrus romanzoffiana* (Arecaceae). Any detached piece of curled bark was a potential *P. australis* nest site.

Other host plants, additional to those in Downes (2015), included the flame tree (*Brachychiton acerifolius*, Malvaceae), frangipani (*Plumeria rubra*, Apocynaceae), mock orange (*Murraya paniculata*, Rutaceae), native mulberry (*Morinda citrifolia*, Rubiaceae), weeping paperbark, (*Melaleuca leucadendra*, Myrtaceae) and powder-puff (*Calliandra haematocephala*, Fabaceae). A notable exclusion was yellow oleander (*Cascabela thevetia* [= *Thevetia peruviana*], Apocynaceae), which grew beside and between plants used for nesting by *P. australis*. Among the unexpected locations of *P. australis* nests were abandoned nests of the green weaver ant, *Oecophylla smaragdina* Fabricius.

External structure
Nests were typically built between living leaves, but could also be constructed on a single flat, folded or curled leaf, living or dead, with lengths ranging from 2-40 cm. Large leaves, *e.g.* those of the umbrella tree *Schefflera actinophylla* (Araliaceae), provided scope for larger than average nests, but did not lend themselves to structured interiors. Complex interior structure was more a feature of nests built on trees with small leaves, *e.g. Calliandra*,

because leaves incorporated into the nest interior necessarily produced complete or incomplete partitions.

Nests could be clustered, *e.g.* six nests in adjacent stems of one banana plant. Sometimes, nests were close (2-3 cm apart) or contiguous, so that the only criterion for their being separate nests was the lack of any internal connection. In one case there was a nest within a nest: an inner partition of (outer-wall) carton separated the interior into two apparently independent areas.
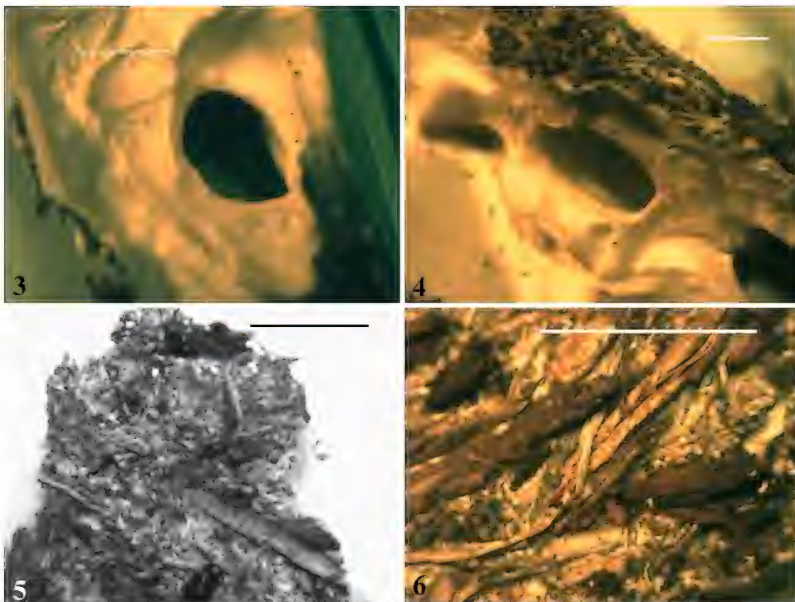

Figs 1-2. Nests of *Polyrhachis australis* Mayr: (1) workers at entrance of nest constructed between two leaves. Scale bar 10 mm; (2) nest incorporating several host plant leaves. Scale bar 20 mm. Photos by Malcolm Tattersall.

Notwithstanding the variety of form, nests could be assigned to one of two broad types on the basis of construction materials. The commonest were nests with dark-coloured exteriors consisting of densely-packed particulate matter (carton) lined wholly or partly by larval silk. The other kind (4.5%) had fine, sparse, particulate plant (and perhaps insect) fragments embedded in cream-coloured, fluffy, three-dimensional masses of convoluted fibres assumed to be spider silk (see Methods), making the nests conspicuously pale and flaccid. Despite their structural weakness, spider-silk nests could be large when hosted by trees with large leaves.

The mean nest size was 32.4 ± 69.9 cm^3, range 1.5-1008 cm^3, n = 355; the median nest size was 14 cm^3. Hence the distribution was positively skewed due to a small number of relatively large nests. The number of occupants, however, correlated only moderately with nest size, $R^2 = 0.47$, n = 302, and the density of ants in nests was similarly affected. See Downes (2015) for more quantified details.

Entrance/exit holes of carton-based nests were *ca* 4 mm in diameter and numbered up to three in large nests. Some had a shallow, raised lip that could be exaggerated to form a squat turret-like structure. Sometimes an interior portal in a partition (see below: internal structure) took the form of an entrance hole, *i.e.* having the same width and with (or without) a raised lip.

Figs 3-6. Nest structure of *Polyrhachis australis* Mayr: (3-4) perforated partitions of reinforced silk inside nest. Scale bars 5 mm; (5) nest carton in form of fine and coarse particulate matter adpressed against silk lining. Scale bar 5 mm; (6) nest carton of admixed particles. Scale bar 1 mm.

Internal structure

Internal nest structure ranged from none to very complex with multiple silk-lined galleries, channels and partitions. Rarely, the silk lining of the exterior walls was reduced or absent. Internal partitions could have one or more perforations that were usually round or oval (Figs 3-4). The form and extent of the partitions could follow the arrangements of the constituent leaves, in which case they were almost invariably silk-lined; but often the partitions were independently formed from thicker, reinforced (*i.e.* multi-layered) silk which could support its own weight independently. Partition perforations could be small or large relative to the size of the partition, so that in some cases the 'partition' was no more than a strut or pillar crossing a wide gap. Partitions were almost always transverse relative to any long nest axis, but could be longitudinal, in one case almost dividing the entire nest internally into an upper and lower tier with connecting holes before breaking down into ragged gaps supported by reinforced silk pillars; in another extending unperforated to the inner end of the nest, forming two blindly-ending chambers only connected at their forward ends. Partition directions were indeterminate in nests without a long axis. Internal partitions occurred in

spider-silk nests as well, but were usually of pale sheet silk (like unbleached paper), not thickly reinforced; they could also be of the same fluffy spider-silk as the nest walls, but if so were toughened, presumably with the same (larval) sheet silk used for 'standard' partitions. The chambers demarcated by the partitions varied widely in size. The antechamber accessed directly from the entrance hole could be large or small relative to nest size. Rarely, the antechamber was a 'false', unoccupied one, lined at its inner end with 'exterior' carton with another entrance hole – *i.e.* the nest had a 'porch'. Only once did exterior carton form a partition deeper in the nest.

The most consistent and consequential feature of the internal structure was the one most logically expected, that host plant leaf size and shape influenced and largely governed the interior nest structure. In general, the smaller the leaf size, the more leaves were incorporated into the interior structure, the more complex that structure became, the greater was the internal surface area and the larger the number of ants able to occupy the nest, relative to the size of the nest (Fig. 2). Up to 10 or 12 *Calliandra* leaflets could be bound within a single nest. In nests of curled-up bark fragments, the curls of bark typically extended into the interior, providing chambers and increased surface area in the form of helical tunnels. Twigs and stems of the host plant could also extend through the nest interior.

Carton and silk

Carton was composed of grasses, bark and other plant material, admixed with soil and mineral debris and adpressed against the silk lining (Figs 5-7). It could be soft or hard, its fragmented matter fine or coarse (Fig. 5). While typically dense, firm, gritty, compact and more or less rigid, it could also be limp, sparsely endowed with grassy fibres and other imbedded or extruding matter (Fig. 7), often sparse enough to be effectively transparent, with ants visible inside. It could be as soft as moist paper, or crisp and dust-dry, and still contain thriving ants and brood.

Flat-sheet silk lining (Fig. 8) is produced by larvae held and manipulated by workers. Especially when against wood, as with the Cocos palm fronds and other curled bark, this silk could be fine and difficult to see but could also truly be absent, leaving the brood against the bare wood. When deficient in a nest of dead and living leaves, it was invariably the dead leaves that were unlined. Spider silk (Fig. 9) typically formed a limp, flocculent mass. It had very little supporting power, gave easily under its own weight and served only to connect leaves, the latter supporting the nest.

A third kind of silk, tough, dry, ductile and sticky, was also occasionally present (Fig. 10). Probably derived from the pupal cocoons of moths, as discussed below, it could be cut easily with scissors but not torn easily by pulling. It occurred as a semi-transparent wall taking up more than half the length of one nest and was encountered in small amounts in several others.
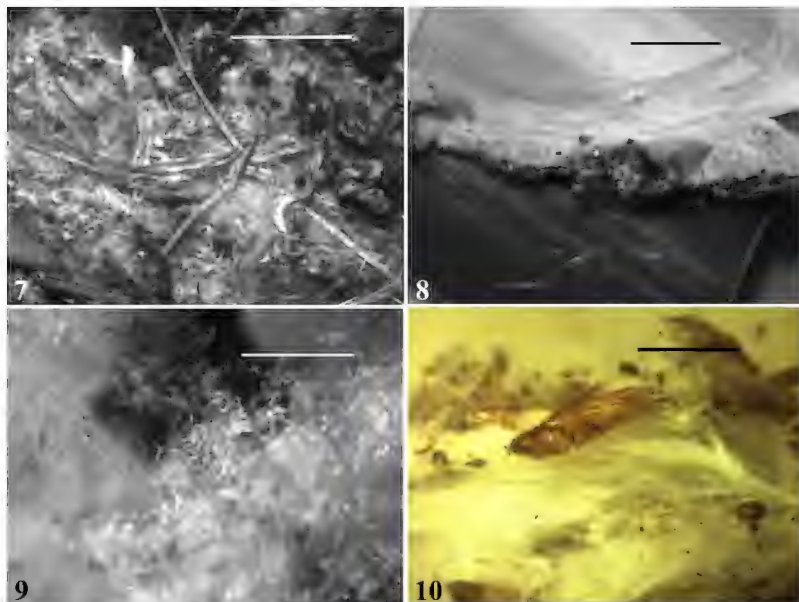
Figs 7-10. Nest structure of *Polyrhachis australis* Mayr: (7) nest carton relatively sparsely packed against inner silk lining visible as a pale swathe from upper left to lower right. Scale bar 5 mm; (8) flat-sheet silk from larvae, lining the carton of nest exterior which is visible along lower edge. Scale bar 5 mm; (9) fluffy (spider) silk inside nest. Scale bar 0.5 mm; (10) ductile moth silk teased out from moth pupal cocoon inside nest. Scale bar 5 mm.
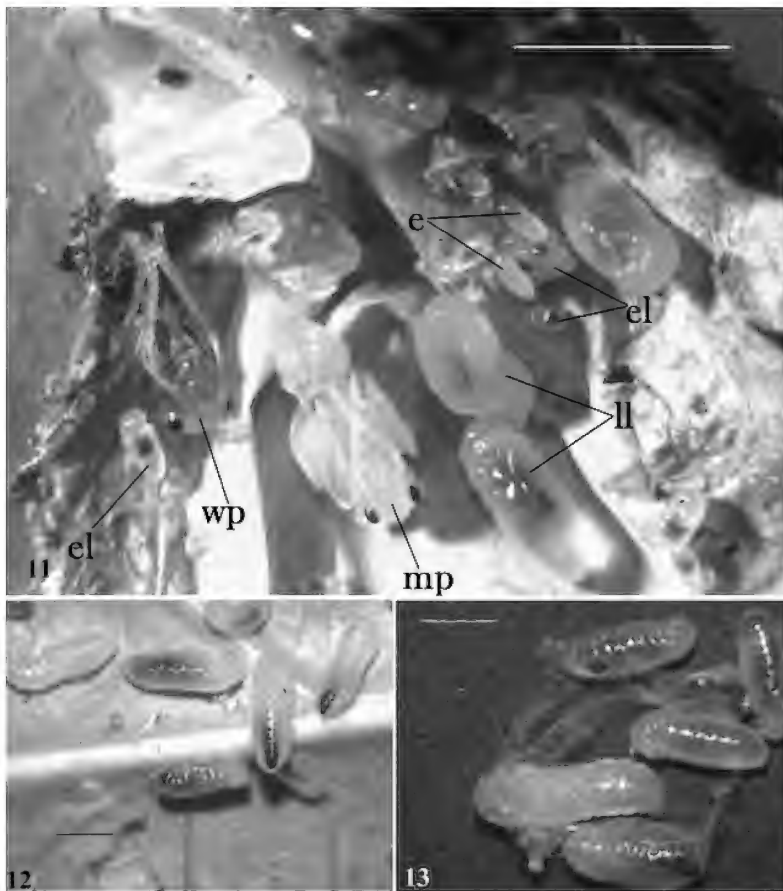
Brood

Dedicated brood chambers were never identified, but clumping of brood was the norm (Fig. 11). These brood clumps could be anywhere except close to a nest entrance. Brood was rarely found in contact with carton, almost always lying on silk lining living leaves or, less commonly, dead leaves and never against unsilked leaves. Most brood, especially larvae, was held against the substrate by loosely applied silk threads of unknown source. These could be effectively invisible, revealed only against a dark background (Figs 12-13).

Longevity and fate

Carton nests were on the whole resistant to rain but were always at risk of damage by rain or wind and, even in dry, windless conditions, they could be breached by falling vegetation. Such damage, when it did occur, inevitably made the ants and their brood vulnerable to invaders. An infestation of the big-headed ant, *Pheidole megacephala* Fabricius, in a breached nest in February 2014 is an example. The fate of a nest was tied to the fate of the foliage hosting it, the oldest observed (15 months) being enclosed by a strong

leaf curled firmly around a stout twig. Of 63 nests tagged and monitored, 31 ended their time naturally with mean longevity 3.4 months. The rest were taken for censusing at known ages. Only five lasted more than a year.

Figs 11-13. Early stages of *Polyrhachis australis* Mayr: (11) brood cluster, including eggs (e), early (el) and late (ll) instar larvae, a worker pupa (wp) and a male pupa (mp). Scale bar 5 mm. (12-13) larvae inside nest: (12) larvae seemingly unattached to the leaf surface. A tear in the silk below the mid-vein reveals attachment between larvae and silk; (13) larvae held to each other and the surface by a loosely-spun web of silk. Scale bars 2 mm.

Most tagged nests remained discrete and autonomous, but some developed a contiguous offshoot or incompletely detached side branch – it was not always

possible to decide which; or a nest would relocate to a new position up to 10 or 15 cm away for no evident reason (this was judged to be a relocation, not a case of budding, if no ants remained in the 'mother' nest). One nest relocated to a loop of the plastic flagging tape marking its location.

Nests did not grow slowly and steadily to a maximum size, as expected. Instead, an initial growth phase of relatively short duration (as little as a week to ten days in some known cases), was followed by a phase typically lasting several months during which the nests decreased in size: of 27 nests for which initial (end of first growth phase, as well as could be judged) and final nest sizes were recorded, mean nest size decreased by 23% (from 13.9 cm^3 to 10.7 cm^3). Once established on certain leaves of the host plant, there was almost no tendency to expand the nest by including other leaves, even when adjacent leaves were close enough. So nests established on trees with large leaves (*e.g.* umbrella trees) reached a large size rapidly and remained large, while those on small-leafed plants did not grow much more, if at all, after enclosing the initial leaves, and hence remained small. There was often no evident reason for the demise of failed nests and perfect, undamaged nests on thriving host leaves were sometimes empty.

Discussion

Host plants and structure

Without data on the relative availability (habitat coverage) of host plants, their relative frequencies, even if available, would be of no value; so a checklist must suffice.

Also, because the nests of many *Polyrhachis* weaver ants, unlike *Oecophylla* F. Smith, show high variability in location and host plants (Dwyer and Ebert 1994, Liefke *et al.* 1998, Robson and Kohout 2007), any list of host plants for *P. australis* becomes less intriguing than plants that are never used despite being available. One such was *Cascabela thevetia*, which never hosted a *P. australis* nest over the 5-year period, showing that host plant selection does not simply reflect relative abundance. *C. thevetia*'s intrinsic toxins may be repellent, or its leaves too narrow (0.5-1.5 cm) for adequate support and concealment. The latter problem has been solved in a unique way by *P. muelleri* Forel: its silk nests are translucent and its larvae are green, camouflaging them against the leaf surface (Dorow *et al.* 1990). A general understanding of nest site selection by ants will require more studies of the sort done by Campbell *et al.* (2013) on arboreal thorn-dwelling ants.

Although arboreal *Polyrhachis* ants may pull and slightly bend a leaf at its edge (Hölldobler and Wilson 1983), they cannot curl leaves into desired positions, because they lack the uniquely cooperative chain-forming behaviours characteristic of *Oecophylla*. Hence we find *P. australis* (and *P. pilosa*) preferentially nesting in the folds of leaves curled either naturally or by agents, especially jumping spiders (Dwyer and Ebert 1994).

The same authors found that by teasing apart strands to provide 'a flocculent mass of fibres', *P. australis* and *P. pilosa* constructed nests entirely of spider silk in the laboratory, when deprived of any other material; while in the field (SE Queensland), the use of spider silk was found to be common and could be extensive. In northern Queensland, nests composed primarily of silk from spider webs or shelters are relatively uncommon but do occur. The sparing use of particulate matter in a nest otherwise made solely of spider silk has also been reported for a rock-dwelling spiny ant, *P. turneri* (Robson 2004).

The number and placement of nest entrances varies widely in *P. australis*, but can be fixed in other species, *e.g. P muelleri* (Dorow *et al*. 1990).

Nest size (volume) was a poor indicator not only of number and hence density of occupants, but also of nest age. Chambers large or small could be occupied or unoccupied and, on this basis alone, volume would not be an expected index of other parameters. Even a moderate correlation of nest size with number of occupants was surprising given the extent to which internal structure governs available surface area.

The nests of some arboreal *Polyrhachis* species contain several chambers, others only a single chamber (Liefke *et al.* 1998). An approximate consistency in the number (6-7) and arrangement of internal chambers may be a feature of nest design in *P. delecta* Kohout (Tranter and Hughes 2015), but larger sample sizes would be needed to confirm this. *P. australis* nests showed no such consistency, responding rather to the constraints and opportunities afforded by the foliage of the host plant. The 'porch' feature in some nests may be a device to buffer the effects of rain and/or invaders. Because queens and other castes relocated during nest dissection, no evidence could be found for the possibility of intranidal oligogyny, that is, the demarcation of separate zones controlled by individual queens. Nothing in the queens' behaviour, however, lent support to the notion that they were territorial.

Carton and silk
The term 'carton', loosely used in the past, is nowadays taken to mean the nest's exterior mass of particulate material, excluding the inner silk lining (Robson and Kohout 2007). However, while the two layers are discrete, silk may be incorporated into the carton layer as well, as reported by Hölldobler and Wilson (1983) for *P. robsoni* Kohout.

Not all arboreal weaver ants of the genus *Polyrhachis* make nests of carton. The nests of *P. bicolor* F. Smith and *P. muelleri*, for example, are made largely or exclusively of loosely woven, pure spun silk, leaving them translucent (Jacobson 1908, Dorow *et al*. 1990, Liefke *et al*. 1998). Some *P. australis* nests are partly translucent when the carton material is minimal.

The production and use of silk for nest building in *Polyrhachis* has a surprisingly labile evolutionary history (Robson *et al.* 2015). It is almost

exclusively a feature of arboreal species and the flat-sheet silk used for interior lining appears to be universally of larval origin in arboreal ants of this genus (Robson and Kohout 2007). *Polyrhachis australis* larvae do not spin pupal cocoons, so the silk they produce is presumably dedicated wholly to nest building and repair. The images of apparently fluffy silk being extracted from an ant larva by two workers (Brisbane Insects 2013) must remain a curiosity pending clearer evidence.

Harvesting and recycling of spider silk by *P. australis* and *P. pilosa* has been directly observed by Dwyer and Ebert (1994), who proposed that the use of spider silk promotes polydomy and hence control of territory and food resources, while obviating the need to expose larvae to desiccation and other hazards when new nests are being initiated. The frequency (12%) with which jumping spiders (family Salticidae) were found with the weaver ants in the present study suggests that a mutualism might exist between them, with *P. australis* preferentially locating in places where these spiders are plentiful.

Several lepidopteran nest associates, in particular a stathmopodine moth symbiotic with *P. australis*, produced silk apparently of material benefit for the ants, perhaps in part offsetting the depredations of the moth larvae.

Brood
Workers were slow to relocate brood during nest dissection, probably because the silk strands anchoring the brood to the substrate had to be cut first. Hence the original clumping of brood was evident. The anchoring would have minimised dislodgment when the nest was buffeted by wind or jarred by falling fronds. Brood anchored by silk strands was also noted by Dorow *et al.* (1990) for *P. muelleri* and by Liefke *et al.* (1998) for several other *Polyrhachis* species. Whether the brood clumps of *P. australis* represent the output of different queens is unknown.

Ants, especially the brood, are particularly vulnerable to infection on account of their social habits and low intracolonial genetic diversity (Graystock and Hughes 2011, Tranter *et al.* 2014). Hence, these social insects keep their nests exceptionally clean (Hölldobler and Wilson 1990). Their larval silk may aid in warding off disease-carrying agents (Fountain and Hughes 2011) and grooming, as well as nest hygiene, plays a part in disease resistance (Fefferman *et al.* 2007). Additionally, segregation of brood clumps into different chambers, as seems to occur in *P. delecta*, could play a part in minimising the spread of harmful agents (Tranter and Hughes 2015). Such segregation was not evident in *P. australis* nests, however.

Longevity and fate
Polyrhachis australis nests are necessarily well adapted to a monsoonal climate, but excessive use of spider silk in their construction increases their vulnerability to rain (Dwyer and Ebert 1994). The common carton form of the nest showed no evidence of being thicker or denser on its uppermost part,

as occurs in the nests of *Camponotus senex* F. Smith (Hölldobler and Wilson 1983). The social structure of *P. australis* populations favours polygyny (Downes 2015), consistent with the suggestion of Oliveira *et al.* (2011) that polygyny in the arboreal ant *Odontomachus hastatus* Fabricius is promoted when nests are liable to destruction by rain.

An understanding (at least my understanding) of the apparently patternless set of nest relocations, size fluctuations, hasty desertions of seemingly perfect nests together with reluctance to abandon other seriously defective ones, to say nothing of how budding as a reproductive strategy operates within these constraints, is a distant prospect. Nest longevity is inseparable from the longevity and changing disposition of the host vegetation and it would be surprising if polydomy was not in some measure driven by these dynamics.

Since nest size (volume) bore no reliable relation to total ant numbers and hence to colony productivity, the lack of nest growth (or even the typical nest shrinkage) in nests monitored for size cannot be taken as indicating any decline in viability.

Acknowledgements

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